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# A SYSTEMATIC STUDY OF THE NORTH AMERICAN GENUS *TRILLIUM*, ITS VARIABILITY, AND ITS RELATION TO *PARIS* AND *MEDEOLA*

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## INTRODUCTION

*Trillium* is a genus in which remarkable uniformity in general appearance and structure is combined with great variability in certain organs from species to species. This variability is of such a nature that it is often difficult to delimit the species accurately according to present knowledge. While the range of variation, in leaf characters, for example, is so slight in the genus that a single leaf can in nearly all cases be recognized at sight as belonging to *Trillium*, yet in many cases it would be quite impossible to determine with certainty the species.

The present paper may therefore be regarded as a conspectus of the North American species of *Trillium*—thirty-one of which, with nine varieties, are recognized—without an attempt to delimit in many cases the exact boundaries of individual species. This can only be done satisfactorily after further extensive field studies of the range of variation in a number of the species.

*Trillium* is of particular interest from another point of view. A number of its species have long been known to give rise to striking variations, such as double flowers, extra leaf whorls, increase in number of parts in a whorl, etc. The references to such cases are very scattered in the literature, but in the second part of this paper an attempt is made to bring them together. While it is quite certain that there are omissions, yet it is hoped that all the more important records have been included. The remarkable variations of *T. grandiflorum* have been most extensively studied, but cases in which extra whorls of leaves occur are perhaps of greater phylogenetic interest. Instances in which a double flower continues to be produced from the same rootstock year

after year indicate that such a rootstock developed from a seed in which a definite germinal change had taken place. The occurrence of double flowers, which was formerly supposed to be a result of cultivation, is now known as a variation in many wild species.

Unless otherwise mentioned, the specimens examined are from the herbarium of the Missouri Botanical Garden where most of the work was done.

#### KEY TO MAP

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|---|--|
| 1. <i>T. discolor</i> Wray  | 16a. <i>T. erectum</i> var. <i>album</i> (Michx.) Pursh              |
| 2. <i>T. stamineum</i> Harb.  | 16b. <i>T. erectum</i> var. <i>viridiflorum</i> Hook.                |
| 3. <i>T. decumbens</i> Harb.  | 17. <i>T. Vaseyi</i> Harb.   |
| 4. <i>T. sessile</i> L.   | 18. <i>T. Rugelii</i> Rendle   |
| 5. <i>T. Underwoodii</i> Small  | 19. <i>T. simile</i> Gleason   |
| 6. <i>T. Hugerii</i> Small  | 20. <i>T. declinatum</i> (Gray) Gleason                              |
| 7. <i>T. luteum</i> (Muhl.) Harb.   | 21. <i>T. cernuum</i> L.   |
| 7a. <i>T. luteum</i> var. <i>latipetalum</i> Gates, n. var.                   | 22. <i>T. undulatum</i> Willd.                                       |
| 8. <i>T. viridescens</i> Nutt.  | 23. <i>T. Scouleri</i> Rydb.   |
| 9. <i>T. viride</i> Beck  | 24. <i>T. grandiflorum</i> (Michx.) Salisb.                          |
| 10. <i>T. Ludovicianum</i> Harb.  | 24a. <i>T. grandiflorum</i> var. trans. <i>variegatum</i> Smith      |
| 11. <i>T. lanceolatum</i> Boykin ex Wats.                                     | 24b. <i>T. grandiflorum</i> var. trans. <i>parvum</i> Gates, n. var. |
| 11a. <i>T. lanceolatum</i> var. <i>rectistamineum</i> Gates, n. var.          | 25. <i>T. ovatum</i> Pursh   |
| 12. <i>T. recurvatum</i> Beck   | 25a. <i>T. ovatum</i> trans. var. <i>stenosepalum</i> Gates, n. var. |
| 13. <i>T. petiolatum</i> Pursh  | 26. <i>T. nivale</i> Riddell   |
| 14. <i>T. giganteum</i> (Hook. & Arn.) Heller                                 | 27. <i>T. rivale</i> Wats.   |
| 14a. <i>T. giganteum</i> var. <i>chloropetalum</i> (Torr.) Gates, comb. nov.  | 28. <i>T. Catesbaei</i> Ell.   |
| 14b. <i>T. giganteum</i> var. <i>angustipetalum</i> (Torr.) Gates, comb. nov. | 29. <i>T. affine</i> Rendle  |
| 15. <i>T. pusillum</i> Michx.   | 30. <i>T. venosum</i> Gates, n. sp.                                  |
| 16. <i>T. erectum</i> L.  | 31. <i>T. obovatum</i> Pursh   |

#### TRILLIUM L.

1. **Trillium discolor** Wray, in Curt. Bot. Mag. *pl.* 3097. 1831.

*T. sessile* var. *Wrayi*. Wats. Proc. Am. Acad. 14: 273. 1879.

This peculiar species is mainly distinguished from the other species of the *T. sessile* group by its very obtuse, broadly spatulate petals (one usually apiculate), which are pale sulphur-yellow inclining to green.

In pine woods, South Carolina, North Carolina, and Georgia. Rare.

2. **T. stamineum** Harb. Biltm. Bot. Studies 1: 23. 1901.

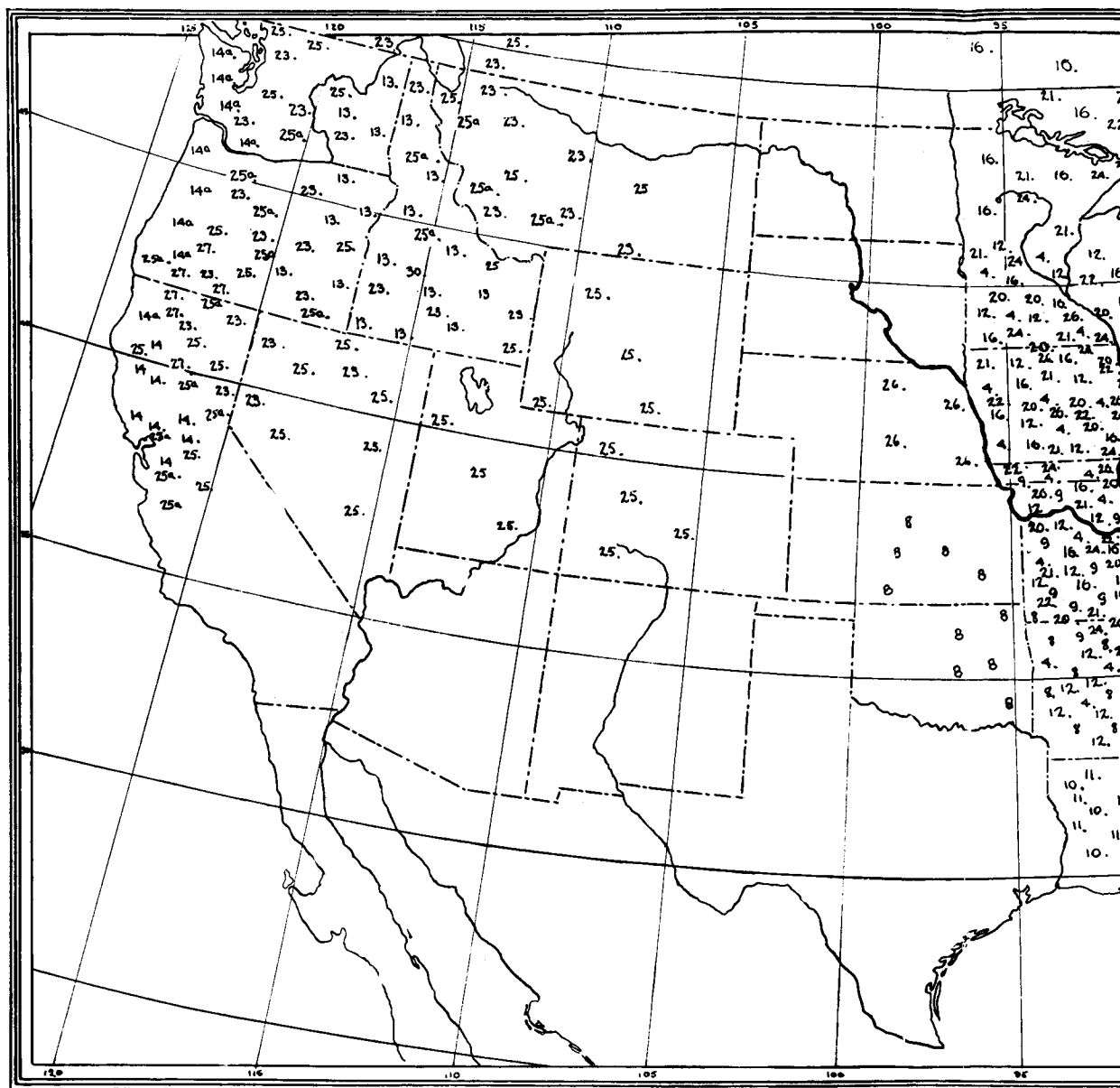
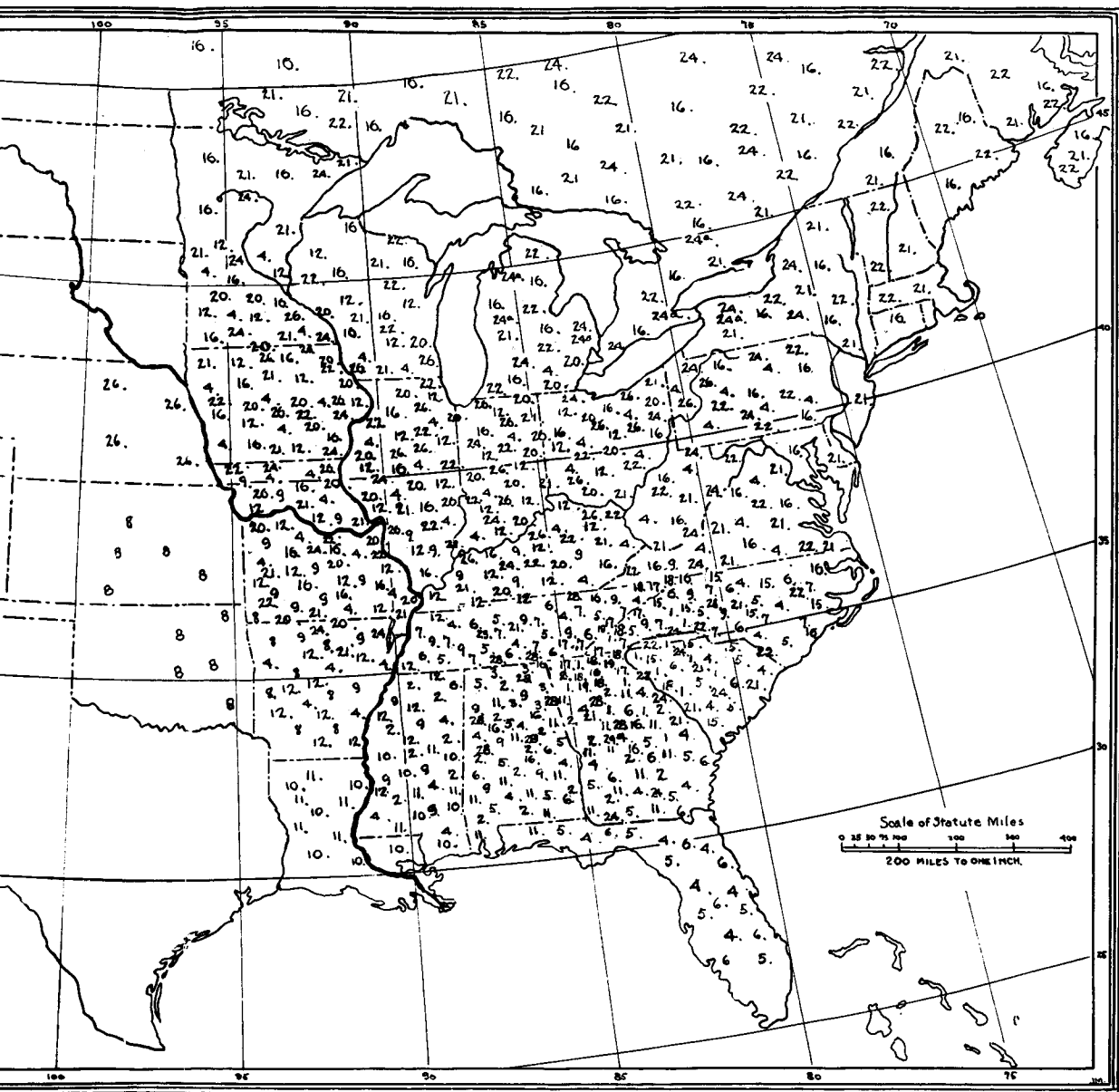


Fig. 1. Map showing distribution of species of



Map showing distribution of species of *Trillium*.

Nearest *T. sessile* but easily recognized by its pubescent stem, widely spreading, twisted petals, unpleasant odor, larger stamens, and very short filaments.

In rocky woods, Georgia, Alabama, and Mississippi.

**3. *T. decumbens* Harb. Biltm. Bot. Studies 1: 158. 1902.**

This species agrees with *T. stamineum* in having a pubescent stem, twisted petals, and very short filaments, and differs from it chiefly in having erect petals, decumbent stem, flowers not fetid, stamens only one-fourth the length of the petals, stigma stout, and a marked prolongation of the anther connective. The last feature occurs in no other known species of *Trillium* except as an occasional variation, but is found more highly developed as a generic character in the genus *Paris*.

In rocky woods, northeastern Alabama.

**4. *T. sessile* L. Sp. Pl. 340. 1753; Curt. Bot. Mag. pl. 40. 1790; Lodd. Bot. Cab. 9: pl. 875. 1824; Fl. Serres 22: pl. 2311. 1877; Redouté, Les Liliacées 3: pl. 133. 1807; Lamarck, Encyc. Meth. 8: 102. 1808; Illustr. Gen. Tab. 2: pl. 267, fig. 1. 1823.**

*Solanum Virginianum triphyllon*, tripetalo flore atropurpureo, in foliorum sinu absque pediculo sessili, Pluk. Alm. Bot. 352. 1696; Phytogr. pl. 111, fig. 6. 1691.

*Solanum triphyllon* Catesb. Nat. Hist. Car. 1: 50. pl. 50. 1754.

In woods, Pennsylvania to Minnesota, south to Florida, Mississippi, and Arkansas.

**5. *T. Underwoodii* Small, Bull. Torr. Bot. Club 24: 172. 1897.**

This species is distinguished from *T. sessile* chiefly by its larger sepals, narrowly oblanceolate, longer petals, which are also longer relatively to the length of the sepals, and by its longer anthers.

In woods and fields, North Carolina to Tennessee, south to Florida and Alabama.

6. **T. Hugerii** Small, Fl. Southeastern U. S. 277. 1903.

This plant differs from *T. Underwoodii* in having leaves suborbicular to broadly ovate, abruptly obtuse-pointed, petals oblong-lanceolate to spatulate, and anthers not subsessile.

In rich woods, North Carolina and Tennessee to Florida.

7. **T. luteum** (Muhl.) Harb. Biltm. Bot. Studies 1: 21. 1901.

Plate 7, fig. 2.

*T. sessile* var. *luteum* Muhl. Cat. 38. 1813.

This is distinguished from *T. Underwoodii* by the yellow color of the petals, ovary, filaments, and anthers; otherwise it is remarkably similar to that species. Intergrading forms which are probably hybrids occur with petals ranging from dark purple to greenish. Forms also occur with yellow petals and purple anthers, or the petals may be purple and the anthers yellow, or only the connectives of the anthers may be purple. These are perhaps independent Mendelian differences which are constantly being interchanged by crossing in the population. The petals also vary in shape, and there are at least two distinct races in this regard, as indicated by the specimens examined. The petals of the following specimens are rather narrowly lanceolate, 5.6 cm. long, 1 cm. wide, with anthers 2 mm. wide.

Knoxville, Tenn., April, 1898, *A. Ruth* 150, four specimens; same locality, April, 1897, *A. Ruth*, two specimens, cotype.

In woods and along streams, North Carolina and Tennessee. The species is said to occur abundantly near Kingston, Tennessee.<sup>1</sup>

7a. **Var. latipetalum** Gates, n. var. Plate 7, fig. 3.

The following specimens differ from the species in having petals which are oblong-obovate, 3–4.4 cm. in length, 1.4–2 cm. wide, and purple anthers scarcely exceeding 1 mm. in width.

Clemson College, Oconee Co., S. C., April 7, 1906, *H. D. House* 1789, two specimens.

Two other specimens on the above sheets represent yet a third type, having leaves broadly oval, deeply mottled, and

<sup>1</sup> Gray, A. Bot. Gaz. 5: 63. 1880.

abruptly pointed, petals apparently greenish yellow and smaller (19 mm.  $\times$  9 mm.), anthers pale, and stem apparently purple. Study of further specimens will probably show this to be a distinct thing. In the blotching of the leaves and in the color of the petals it resembles *T. viride*.

Thus, although *T. luteum* has a very limited range, it evidently contains a considerable number of intercrossing races or variations showing unit differences.

8. ***T. viridescens*** Nutt. Trans. Am. Phil. Soc. II. 5: 155. 1837.

*T. sessile* var. *Nuttallii* Wats. Proc. Am. Acad. 14: 273. 1879.

*T. sessile* var. *viridescens* Trelease, Rept. Ark. Geol. Surv., 1888. 4: 225. 1891.

This species agrees with *T. viride* chiefly in its pubescence and narrow petals. It may have originated independently from another member of the sessile group. From *T. viride* it differs most markedly in its larger size, its acuminate leaves, and its mostly purple or red petals.

On hillsides and in rich copses, Kansas and Arkansas.

9. ***T. viride*** Beck, Am. Jour. Sci. 11: 178. 1826.

This plant is distinct in many features, especially the linear or linear-elliptic, purplish green, clawed petals, and the oblong to ovate, relatively small, 3-5-nerved leaves mottled with whitish spots. The stem is rough-pubescent at the top, and the leaves more or less pubescent on the veining beneath. It is considered to be most nearly related to *T. recurvatum*.

In woods, Missouri to North Carolina, Alabama, and Mississippi.

10. ***T. Ludovicianum*** Harb. Biltm. Bot. Studies 1: 23. 1901.

According to Harbison, this species is nearest *T. viride* and *T. lanceolatum*. From the former it is separated chiefly by its smooth stem, and from the latter by its shorter stem, broader leaves and sepals, shorter filaments, and straight anthers.



In low, rich woods, Louisiana and Mississippi.

11. ***T. lanceolatum*** Boykin ex Wats. Proc. Am. Acad. 14: 273. 1879.

*T. recurvatum* var. (?) *lanceolatum* Wats. Proc. Am. Acad. 14: 273. 1879.

The most striking peculiarities of this species are its slender and usually tall (1-4 dm.) stem, leaves lanceolate or elliptic and strongly blotched, petals linear or linear-oblong, clawed, and filaments as long as the more or less incurved anthers. It is most nearly related to *T. recurvatum*.

Moist woodlands and river bottoms, Georgia to Alabama and Louisiana.

11a. Var. ***rectistamineum*** Gates, n. var.

Several sheets in the Chapman Herbarium (Mo. Bot. Gard. Herb.) with the number 3869, but without locality, agree with *T. lanceolatum* in foliage except that the leaves are larger (8-10 cm. long) and have much shorter (about 10 cm.), stouter stems. They differ from *T. lanceolatum* conspicuously in the petals, which are broadly lanceolate, tapering at the base but not clawed, 4 cm. long, 18 mm. wide, and dark purple. The sepals are lanceolate, larger than in *T. lanceolatum*, 3 cm. long, 1 cm. wide. The anthers are straight, purple, 2 mm. wide, 9 mm. long, filaments short; the ovary large (8 mm.), styles spreading and recurved. This plant, no doubt, constitutes a distinct species, differing from *T. lanceolatum* especially in the petals, anthers, and ovary, but as the specimens available are without locality and only one shows a complete flower, it seems desirable merely to designate this form as above indicated.

The following specimens probably belong to this variety, although the essential flower characters are not exhibited: Aspalaga, Fla., March, 1897, *Herb. Chapman*, two specimens; Aspalaga Bluff, Gadsden Co., Fla., March 8, 1909, *Roland M. Harper 25*.

12. ***T. recurvatum*** Beck, Am. Jour. Sci. 11: 178. 1826.

*T. unguiculatum* Nutt. Trans. Am. Phil. Soc. II. 5: 154. 1837.

This species agrees with *T. lanceolatum* in its tall stems, which are, however, frequently stout, and incurved anthers. It differs in that the filaments are about half the length of the anthers, the leaves ovate-lanceolate, oval or suborbicular, and narrowed into a petiole of variable length. This last feature suggests *T. petiolatum* in which the petioles are, however, usually much longer. This condition has perhaps originated independently in both species through parallel mutations, an interpretation which is greatly strengthened by the fact that similar petioled leaves occur as a variation in *T. grandiflorum* (see page 78).

In woods, Ohio to Minnesota, south to Mississippi and Arkansas.

13. *T. petiolatum* Pursh, Fl. Am. Sept. 1: 244. 1814; Hook. Fl. Bor. Am. 2: 180. *pl.* 192. 1840.

The very short and stout stem with leaves ovate-elliptic to reniform, and petioles as long as, or longer than, the blades, characterize this remarkable species which is in many respects a parallel to *T. grandiflorum* var. *variegatum*. One feels that the former must have originated in connection with a mutation, as the latter obviously has done. *T. petiolatum* differs from *T. recurvatum* not only in the above features but also in its narrowly oblanceolate petals and straight anthers with shorter filaments.

Idaho, eastern Washington, and eastern Oregon.

14. *T. giganteum* (Hook. & Arn.) Heller, Bull. S. Cal. Acad. 2: 67. 1903.

*T. sessile* var. *giganteum* Hook. & Arn. Bot. Beechey's Voy. 402. 1841.

*T. sessile* var. *Californicum* Wats. Proc. Am. Acad. 14: 273. 1879; Gard. & For. 3: 320. *fig.* 44. 1890, white form.

*T. giganteum* is undoubtedly distinct from the eastern *T. sessile*, being constantly much larger in all its parts. The nature and cause of its gigantism is a very interesting ques-

tion. Through the kindness of Dr. T. H. Goodspeed I was able to examine some histological preparations of the young buds of *T. giganteum* and *T. ovatum*. From such examination as I was able to make I could detect no difference between the two species either in chromosome number or in size of cells. It therefore appears probable that the gigantism of *T. giganteum* is a result of increased growth and multiplication of cells rather than increase in the size of the cell unit. I speak guardedly, however, because my comparison was hasty and incomplete.

*T. giganteum* is characterized by its stout stem, large, round-ovate leaves frequently as broad as long, reaching a length (in specimens observed) of 16 cm. and a width of 12–16 cm. The petals typically are narrowly ovate to lanceolate (extreme size 11 cm.  $\times$  32 mm.), maroon-purple, and the filaments are short, the anthers reaching 2 mm. in length, purple. Mrs. R. M. Austin's No. 19, collected at Butte Creek, near Colby, Butte Co., Cal., July, 1896, agrees with the type except that the petals are white and the leaves constricted at base into a short petiole.

The species extends apparently from Lake and Placer Counties, California, southward to San Luis Obispo County. Particular variations are found most commonly or exclusively in certain localities.

**14a. Var. *chloropetalum* (Torr.) Gates, comb. nov.**

Plate 7, fig. 1.

*T. sessile* var. *chloropetalum* Torr. Pac. Rail. Rept. 4: 151. 1856.

*T. chloropetalum* Howell, Fl. N. W. Am. 1: 661. 1902, in part.

Washington to California, in the coast region.

The variety *chloropetalum* with greenish petals, originally described by Torrey as *T. sessile* var. *chloropetalum* from the "Redwoods," California, is stated by Jepson to be "common on the peninsula of Pt. Reyes in Marin Co." Torrey's diagnosis was "petalis viridulis obovato ellipticis, obtusiusculis, sepala duplo superantibus." The petals in specimens

may be greenish, yellowish, white, or pink, and they also vary in width. In the Napa Valley mostly the white-flowered form occurs. The anthers are yellow.

*T. chloropetalum* Howell, of Oregon and northern California, differs markedly in having oblanceolate, obtuse, white, erect petals 3–4 lines wide and should therefore probably receive a new and distinct specific name. It is represented by the following specimens:

California: Scott River, Siskiyou Co., April 25, 1910, *Geo. D. Butler 1242* (Mo. Bot. Gard. Herb.); Humbug Creek, April 3, 1910, *Geo. D. Butler 1168* (Mo. Bot. Gard. Herb.), petals 5 cm. long, 15 mm. wide, obtuse; near Hupa, Humboldt Co., 1902, *Mrs. M. H. Manning* (Univ. Cal. Herb., 30093); near Arcata, Humboldt Co., April 2, 1905, *Joseph P. Tracy 2155* (Univ. Cal. Herb., 146219); Buck Mountain, Humboldt Co., June 17, 1913, *J. P. Tracy 4181* (Univ. Cal. Herb., 175295).

In some cases the petals are purple except near the base, as in the following specimens:

California: Loma Prieta, eastern slope, April 4, 1894, *J. B. Davy 468* (Univ. Cal. Herb., 4014); Olema, Marin Co., March 31, 1894, *J. B. Davy 679* (Univ. Cal. Herb., 4015). Occasionally the petals are purple only at the tip.

Crystal Springs Lake, San Mateo Co., March 30, 1902, *C. F. Baker 431*, the collector remarks: "This white or pinkish flowered *Trillium* is the predominant form in moist thickets about the lake, but few purple flowered *Trilliums* being seen here." The petals are also narrow, as in the typical var. *chloropetalum*.

**14b. Var. *angustipetalum* (Torr.) Gates, comb. nov.**

Plate 8.

*T. sessile* var. *angustipetalum* Torr. Pac. Rail. Rept. 4: 151. 1856.

The variety *angustipetalum* of Torrey apparently occurs as a variation throughout the range of the species. In other words, the petals vary in width from 2 mm. to 32 mm., and the variation is apparently continuous. Torrey characterized the variety as follows: "foliis basi subito contractes; petalis

lanceolato-linearibus acutis, sepala purpurea fere duplo superantibus. Wet ravines, Washington Mammoth Grove; May 15." It is possible that the narrow-petaled forms predominate in certain localities, e.g., the Sierra Nevadas and about San Luis Obispo County.

The varieties *chloropetalum* and *angustipetalum* therefore represent two independent and continuous series of variations in the petals of *T. giganteum*.

**15. *T. pusillum*** Michx. Fl. Bor. Am. 1: 215. 1803; Rendle, Jour. Bot. 39: 334. *pl. 426, fig. A.* 1901.

*T. pumilum* Pursh, Fl. Am. Sept. 1: 245. 1814.

?*T. Texanum* Buckl. Acad. Phil. Proc. 12: 443. 1861.

This species forms a transition from the sessile-flowered species, of which *T. sessile* may be regarded as the type, to the pedunculate species such as *T. erectum*. Its flower may be quite sessile or on a pedicel 6 mm. in length, as represented by specimens in Herb. Gronovius and Herb. Linnaeus.<sup>1</sup> According to Small,<sup>2</sup> the pedicel is 1 cm. in length. *T. pusillum* is perhaps most nearly related to *T. erectum*, from which it may have been derived. It differs from that species in its smaller and more slender stature, the thickness of the stem scarcely exceeding 1 mm.; also its leaves are oval to lanceolate, obtuse, the petals delicate, smaller (1.4–2 cm. long), pink instead of purple-brown, and the stamens slightly shorter than in *T. erectum*. The stigmas are united at the base to form a style about 2 mm. long, as in *T. Catesbaei* and *T. affine*. It is probable that Buckley's plant represents a distinct form.

In pine lands, North Carolina and South Carolina.

**16. *T. erectum*** L. Sp. Pl. 341. 1758; Curt. Bot. Mag. *pl. 470.* 1800; Lamarck, Encyc. Meth. 8: 102. 1803; Illustr. Gen. Tab. 2: *pl. 267, fig. 2.* 1823; Lodd. Bot. Cab. 19: *pl. 1838.* 1832; Fl. Serres 10: 56. *pl. 990.* 1854–5.

*T. rhomboideum* Michx. Fl. Bor. Am. 1: 215. 1803; Redouté, Les Liliacées 3: *pl. 134.* 1807.

<sup>1</sup> Rendle, A. B. Notes on Trillium. Jour. Bot. 39: 334, 335. 1901.

<sup>2</sup> Fl. Southeastern U. S. 278. 1903.

*T. foetidum* Salisb. Parad. Lond. *pl.* 35. 1805.

*T. erectum* var. *atropurpureum* Pursh, Fl. Am. Sept. 1: 245. 1814; Hook. Fl. Bor. Am. 2: 180. 1840.

*T. purpureum* Kin, in Ell. Sketch 1: 430. 1817.

*T. atropurpureum* Curt. ex. Beck, Bot. N. & M. States, 361. 1833.

*T. erectum rubrum* Clute, Am. Botanist 9: 76. 1905.

Leaves characteristically rhombic, acuminate at the apex, and more or less cuneate at the base; flower fetid, the petals lanceolate or ovate-lanceolate (2.5–4 cm. long), brown-purple, filaments 3–4 mm. in length, nearly as long as the anthers.

In woods, Nova Scotia to Manitoba, south to North Carolina and the mountains of Georgia, Alabama, and Missouri.

**16a.** Var. *album* (Michx.) Pursh, Fl. Am. Sept. 1: 245. 1814; Curt. Bot. Mag. *pl.* 1027. 1807; Lodd. Bot. Cab. 19: *pl.* 1850. 1832.

*T. album* Small, Fl. Southeastern U. S. 278. 1903, and ed. 2, 1913.

*T. rhomboideum* var. *album* Michx. Fl. Bor. Am. 1: 215. 1803.

The unit variety *album* occurs sporadically, differing from the species only in pigmentation, the petals being white and the stamens and ovary whitish or pink (e.g. Westville, Conn., May 9, 1885, *W. A. Setchell* [Univ. Cal. Herb., 3974]; Penn., *James Galen* 189 [Univ. Cal. Herb., 3971]). Another series of variations, however, runs to an extreme in a form recognized by Small as a separate species, *T. album*. This differs not only in having white or pinkish petals which are less inclined to be acuminate, but in its smaller flowers and longer anthers (8–11 mm. long) with pale connectives colored like the filaments. There are thus two independent series of variations: one a negative mutation in loss of color without any other change, the other a more gradual transition toward a white flower, accompanied by decrease in size of flower, increase in length of anthers, and other changes, the extreme condition being recognized as *T. album* Small.

Occurs sporadically and occasionally throughout the range of the species.

In addition to the white variety, various intermediate shades of color occur. *T. obovatum* Pursh probably represents one of these, or it may belong with *T. grandiflorum*. It appears probable that these are original variations, and not the result of crosses between the extremes, though the pure white form probably appears directly as a mutation. Specimens from Oswego, Ithaca, and Utica, N. Y., Mt. Carmel, Ill., southern Pennsylvania, Cincinnati, O., and Hennepin Co., Minn., show various intermediate shades, and some from Port Huron, Mich. and other localities are pale purple.

**16b.** Var. *viridiflorum* Curt. Bot. Mag. *pl.* 3250. 1833.

*T. erectum* var. *γ. petalis ochroleucis* Hook. Fl. Bor. Am. 2: 180. 1840.

*T. erectum* var. *ochroleucum* Hook. ex Macoun, Cat. Canadian Pl. 4: 49. 1888.

*T. pendulum* Willd. Ges. Naturforsch. Fr. Berlin, Neue Schr. 3: 421. 1801; Hort. Berol. *pl.* 35. 1816.

Willdenow's figure differs from that in the 'Botanical Magazine' in having the leaves acuminate instead of obtuse. The flowers are also probably smaller.

Rare. Near Annapolis, Nova Scotia, *Macoun* (Cat. Canadian Pl. 1: 48. 1888.). Macoun also mentions a rare form with green petals from Peterboro Co., Ontario.

**17.** *T. Vaseyi* Harb. Biltm. Bot. Studies 1: 24. 1901.

This plant may be distinguished from *T. erectum* by its "long, slender filaments, smaller stigmas and peduncle, which is deflexed beneath the leaves before anthesis." The flowers are larger and are said by Small often to have a rose-like fragrance, the sepals to be more or less involute above the middle, and the petals ovate or orbicular-ovate, 4-6 cm. in length. Judging from specimens, the plant is also usually larger than *T. erectum*, from which it was probably derived.

Moist woods in high mountains, North Carolina, Tennessee, Georgia, and in Connecticut.

Specimens examined in Mo. Bot. Gard. Herb:

Tomassee Falls, Oconee Co., S. C., 5 May, 1896, *H. D. House* 2094, three specimens; border of Bear Pond, French Mt. (?), 15 May, 1891, *Herb. Chapman*, three sheets. These specimens appear to run into *T. erectum*. Southington, Conn., 30 April, 1897, *C. H. Bissell* 211 (2685). This specimen extends considerably the range of *T. Vaseyi*.

Forma *album* House, Muhlenbergia 6: 73. 1910.

This specimen, from Pigeon Gap, Haywood Co., N. C., has pure white petals, though the anthers and pistil are of the normal purple color.

18. *T. Rugelii* Rendle, Jour. Bot. 39: 331. *pl.* 426, *fig.* B. 1901.

This plant agrees with *T. erectum* and *T. Vaseyi* in leaf-shape and resembles the latter in its nodding peduncle. It differs from them in the petals, which are white, round-ovate, the same length and thrice the breadth of the sepals. The filaments are also only one-third the length of the anthers, which are purple. I have seen no specimens of this species.

In the mountains of western North Carolina and northern Georgia.

19. *T. simile* Gleason, Bull. Torr. Bot. Club 33: 391. 1906.

This species differs from *T. Rugelii* in its "much longer stamens, yellow anthers and proportionately longer filaments" ( $\frac{1}{2}$  as long as the anthers).

Three localities near the border of North Carolina and Georgia.

20. *T. declinatum* (Gray) Gleason, Bull. Torr. Bot. Club 33: 389. 1906.

*T. erectum* var. *declinatum* Gray, Manual, ed. 5, 523. 1868.

This species is apparently more nearly related to *T. cernuum* than to *T. erectum*. Unlike the latter species, it has a pleasant, not fetid, odor. From *T. cernuum* it differs in the declined rather than reflexed peduncle, and in the petals,



which are ovate-oblong and always white, while in *T. cernuum* they may be elliptic, oval or ovate, acute, and white or pink. The anthers and capsule of *T. declinatum* are yellow. Like many species of *Trillium*, it varies greatly in size.

Ohio and southern Michigan to Missouri and Minnesota.

The following specimens from Mo. Bot. Gard. Herb. show interesting peculiarities:

Taughannock Falls, Ithaca, N. Y., 14 May, 1892, *H. von Schrenk*. This specimen agrees with *T. declinatum* except that the capsule is purple, the peduncle appears to be erect, and the petals are lanceolate. It may be a white derivative from *T. erectum*. Fountaindale, Winnebago Co., Ill., 1867, *M. S. Bebie* 8229; Armstrong, Emmet Co., Ia., 13 May, 1899, *R. I. Cratty*. These specimens differ from *T. declinatum* in having purple anthers. The former also has narrowed petals. These are perhaps unit variations, and they show that the coloration of petals, anthers, and capsule may vary independently, but in some specimens certain organs are only partly colored.

**21. *T. cernuum* L.** Sp. Pl. 339. 1753; Curt. Bot. Mag. *pl.* 954. 1806; Barton, Fl. N. Am. 2: 13. *pl.* 40. 1822; Meehan's Monthly 10: 49. *pl.* 4. 1900.

The main peculiarities of this species were mentioned under *T. declinatum*. Its foliage is closely similar to that of other members of the *erectum* group.

In rich woods, Nova Scotia to Minnesota, Georgia, and Missouri.

**22. *T. undulatum* Willd.** Ges. Naturforsch. Freunde Berlin, Neue Schr. 3: 422. 1801.

*T. erythrocarpum* Michx. Fl. Bor. Am. 1: 216. 1803; Sweet, Fl. Gard. 3: *pl.* 212. 1827; Lodd. Bot. Cab. 13: *pl.* 1232. 1827; Curt. Bot. Mag. *pl.* 3002. 1830. In this last figure the leaves have short petioles.

*T. pictum* Pursh, Fl. Am. Sept. 1: 244. 1814.

This species is somewhat isolated from its nearest relatives by a number of peculiarities. The leaves are ovate,

acuminate, rounded at base, with a petiole varying in length from 3 to 20 mm. The petals are oblong or oval to obovate, much longer than the sepals, white, striped with purple, particularly at the base, the margins waved. The anthers are short (about 5 mm.), as long as the filaments, shorter than the stigmas, and apparently reddish. In these features it agrees with *T. cernuum*. The berry is red, whence the name of Michaux.

In swamp woods and bogs, Nova Scotia to Wisconsin, south to Missouri, and in the mountains to South Carolina and Georgia.

**23. *T. Scouleri*** Rydb. Bull. Torr. Bot. Club **33**: 394. 1906.

*T. grandiflorum* Hook. Fl. Bor. Am. **2**: 180. 1840, in part.

*T. obovatum* Hook. *ibid.*, in part.

This species, *T. grandiflorum*, and *T. ovatum* agree in their main features, especially in flower structure, all having rather broad, white petals. The two western species are widely distinct from *T. grandiflorum*, from which they must therefore have separated long ago. *T. Scouleri* differs from *T. grandiflorum* in the shape of the leaves, which are broadly rhomboid, rounded or truncate at base, and in the petals which are ovate-oblong, subacute.

British Columbia to Montana and California.

**24. *T. grandiflorum*** (Michx.) Salisb. Parad. Lond. *pl.* **1**. 1805; Lodd. Bot. Cab. **14**: *pl.* **1349**. 1828; Regel, Gartenfl. **17**: 98. *pl.* **575**. 1868; Garden **36**: 394. *fig.* **1**. 1889; *ibid.* **40**: 222. *pl.* **821**. 1891; Fl. Serres **10**: *pl.* **991**. 1854–5; Meehan's Monthly **4**: 17. *pl.* **2**. 1894; Traill, Stud. Pl. Life in Canada, **35**. *pl.* **3**. 1906; Rendle, Jour. Bot. **39**: 330. 1901.

*T. rhomboideum* v. *grandiflorum* Michx. Fl. Bor. Am. **1**: 216. 1803.

*T. erythrocarpum* Curt. Bot. Mag. *pl.* **855**. 1805.

This species is markedly characterized by (1) its oval or rhombic-oval, acuminate leaves, more or less cuneate at the sessile or constricted base, (2) its large, oblanceolate or obovate-oblanceolate, erect-spreading petals (reaching 7 ×

3.5 cm.) exceeding the much narrower sepals, crisped, white or sometimes pink, rarely green,<sup>1</sup> (3) the berry red, becoming black. *T. grandiflorum* also differs from the two western species in having the stigma lobes erect, spreading or connivent, much exceeded by the stamens. Another interesting feature is the unilocular ovary, referred to by Salisbury and confirmed by Rendle, who also quotes Mr. Smith of Newry to the effect that there are two very similar forms of *T. grandiflorum*, one of which grows in bogs and the other in dry soil. Compared with *T. erectum*, the ovary of *T. grandiflorum* is much smaller and white, though deeply six-lobed as shown in Salisbury's plate.

Woods and hillsides, Quebec to Minnesota and Missouri, south along the mountains to Florida.

**24a.** Var. trans. **variegatum** Smith, Bot. Gaz. 4: 181. 1879.  
*T. grandiflorum* Plant World 6: 89. fig. 1. 1903.

This remarkably variable condition of *T. grandiflorum* was described by Smith from Michigan and has been redescribed many times since. It is particularly common in southwestern Ontario, in the Don Valley and elsewhere, and Buffalo and Syracuse, N. Y. (See variation of *Trillium*, p. 72.) In size it appears to be constantly smaller than *T. grandiflorum typica* and to agree with var. *parvum*.

**24b.** Var. trans. **parvum** Gates, n. var.

Omnino forma typica convenit excepto parvitas omnibus partibus (stipa, folia floraque) et petalibus puniceibus fierens.

I have recently had the opportunity of studying living plants of a variety of *T. grandiflorum* obtained by the Missouri Botanical Garden from Exeter, New Hampshire, where a quantity of the rootstocks were dug up in 1914 by L. E. Williams. They differ from the type of *T. grandiflorum* in nothing except their constantly smaller size and in the fact that they begin to turn pink very soon after opening. Their description is as follows:

<sup>1</sup>A specimen of *T. grandiflorum* with yellow petals has been reported from Galt, Ontario. (Am. Bot. 12: 83. 1907.)

Rootstock horizontal, stem sheathed at base for 2–3 cm., green, usually reddish near the base, smooth, 10–15 cm. high, 4–6 mm. in thickness at base, tapering gradually to 2–3 mm. at the top; leaves rhombic-oval or rhombic-ovate, 4–7 cm. long, 3–6 cm. wide, sessile or nearly so, acute, acuminate; peduncle 2–3 cm. in length, erect, flower bent horizontally; sepals lanceolate, acute or acuminate, 2–3.5 cm. long, 9–14 mm. wide; petals forming a tube at base, spreading above, margin waved, oblanceolate to obovate-oblanceolate, obtuse or broadly acute, sometimes minutely emarginate, 28–44 mm. long, 13–22 mm. wide, white at first, soon changing to pale pink and fading to purplish pink, considerably exceeding the sepals; stamens adnate to base of the petals, filaments white, 5–6 mm. long, anthers 5–10 mm. long; ovary 6–8 mm. long, 6-angled, winged, white, three parietal placentae sometimes nearly meeting in the center, stigmas slender, erect-spreading, 3–4 mm. long.

Specimens examined in Mo. Bot. Gard. Herb.:

Exeter, N. H., March, 1915, *L. E. Williams*, TYPE; Alma, Mich., May 9, 1891, *Chas. A. Davis*; without locality, *E. C. Smith*, two sheets; Edgebrook, Cook Co., Ill., May 11, 1897, *Agnes Chase*, four specimens; Chautauqua, N. Y., May, 1909, *Mrs. C. P. Damon*; Ithaca, N. Y., April 24, 1891, *H. von Schrenk*; Battersea, Ont., May 31, 1893, *J. Fowler*, two specimens; Mountville, (Ohio?), May, 1889, *Mrs. Eby*; Middlebury, Vt., May 3, 1878, *Ezra Brainerd*, three specimens.

**25. *T. ovatum*** Pursh, Fl. Am. Sept. 1: 245. 1814.

*T. californicum* Kellogg, Proc. Cal. Acad. 2: 50. fig. 2. 1860.

*T. crassifolium* Piper, Erythea 7: 104. 1899.

*T. obovatum* Hook. Fl. Bor. Am. 2: 180. 1840.

This species was described by Pursh as follows: “*T. pedunculo erecto, petalis oblongis acutis patentibus calyce lineari paulo longioribus, foliis ovatis sensim acutis arcte sessilibus. On the rapids of Columbia River. M. Lewis. 4 April. v. s. Flowers pale purple.*” The characters of *T. ovatum* must be determined by specimens from the original region. Such specimens have fairly broad sepals and are in-

intermediate in this respect between *T. venosum* and *T. ovatum* var. *stenosepalum*.

*T. ovatum* may be distinguished from *T. grandiflorum* by its usually narrower and lanceolate petals, which are acute, and color soon changing to rose and dark red. According to Mr. T. Smith of Newry, England,<sup>1</sup> *T. ovatum* opens its flowers earlier, soon after emerging from the ground. Another important difference as regards many specimens is the much shorter stamens (anthers about 6 mm.). This feature is not constant, however, for in some specimens the anthers reach 10 mm. as in *T. grandiflorum*, and there are also intermediate lengths. In his 'Flora of Montana' Rydberg records this species with the statement that the petals are purplish or dark rose-colored, oblanceolate, acute, the sepals narrow and the peduncles very slender.

British Columbia to Montana, Colorado, and California (to Santa Cruz).

Specimens examined:

Washington: Stevens Pass, Cascade Mountains, Aug. 17, 1893, *Sandberg & Leiberg 770* (Univ. Cal. Herb., 170660), leaves  $17 \times 13.5$  cm., sepals 19 mm. wide; Tacoma, May 3, 1908, *J. B. Flett 3430* (Univ. Cal. Herb., 128157); Cascade Tunnel, alt. 3500 feet, July 15, 1911, *M. E. Jones* (Univ. Cal. Herb., 175870), differs from *T. venosum* chiefly in having leaves ovate-rhomboid, not oval, and petals turning purple; *R. H. Platt 189* (Univ. Cal. Herb., 3985).

California: Dinsmore's ranch, in valley of Van Duzen River opposite Buck Mountain, Humboldt Co., June 26, 1913, *J. P. Tracy 4350* (Univ. Cal. Herb., 175281); Sherwood Valley, May 29, 1899, *W. C. Blasdale 1039* (Univ. Cal. Herb., 30092), sepals narrowish, 6 mm., petals drying purple; Comptche, Mendocino Co., June, 1906, *H. A. Walker 300* (Univ. Cal. Herb., 112751), leaves  $17 \times 14.5$  cm., sepals 18 mm. wide; near Ukiah, 1897, *Carl Purdy* (Univ. Cal. Herb., 3993); San Leandro Creek, Oakland Hills, San Francisco Bay, March 23, 1901, *H. M. Hall 875* (Univ. Cal. Herb., 3987); Aptos,

<sup>1</sup> See Rendle, A. B. Notes on Trillium. Jour. Bot. 39: 331. 1901.

April 14, 1903, *C. F. Baker 3010* (Univ. Cal. Herb., 142145), same as Sherwood Valley specimen.

The line between *T. ovatum* and var. *stenosepalum* is not very sharply defined. The differences are discussed under var. *stenosepalum*.

**25a.** Var. trans. *stenosepalum* Gates, n. var. Plate 6, fig. 2.

Herba glabra, foliis parvis, ovatis, 5-nerviis, breviter acuminate, ad basim rotundo in petiolo perbreve constricto; pedunculo erecto; sepalis brevibus, lanceolatis, acuminate, 13–33 mm. longis, 3.5–6 mm. latis; petalis albis, oblongo-obovatis, obtusis, marginibus undulatis, sepalis multum excedentibus; antheribus 8 mm. longis, flavis stigmatibus multum excedentibus; stigmatibus perbrevibus, tenuis, apicibus recurvatis.

Rootstock horizontal; stem rather slender, 19–30 cm. in length, 3–9 mm. in thickness, purplish above the base, which is sheathed for 3–5 cm.; leaves ovate, 5-nerved, 5.5–10 cm. long, 4.5–7.5 cm. broad, acute, short-acuminate, rounded at the base and sharply constricted into a very short petiole; peduncle about 2–6.5 cm. in length, erect, 1 mm. thick; sepals lanceolate, acuminate, about 13–33 mm. long, 3.5–6 mm. wide, delicate; petals white, oblong-obovate, obtuse, margin somewhat waved, 20–43 mm. long, 10–15 mm. broad; anthers yellow, straight, 8 mm. long, much exceeding the stigmas, filaments 5 mm. long, very slender; stigmas very short (2–3 mm.), slender, nearly erect, tips recurved, ovary yellow, and about 5 mm. in length. The three veins in the sepals are very inconspicuous and in small specimens are only visible with a lens.

This strikingly distinct variety stands between *T. Scouleri* and *T. grandiflorum* in certain respects but shows a number of peculiarities. The leaves resemble those of *T. Scouleri* but are not as small as the minimum size in that species, and scarcely rhomboid. The flowers resemble those of *T. grandiflorum* but are smaller in all their parts. The sepals in particular are greatly reduced in comparison with the petals. The variety *stenosepalum* is separated from *T. venosum* not

only by the entirely different sepals, but by the straight yellow anthers, the very much shorter stigmas, and slightly in the shape of the leaves.

The variety *stenosepalum* is nearly related to *T. ovatum*, and all the specimens cited from Californian localities have hitherto been included under the latter species. It is impossible, however, to include under one name forms which differ so widely, especially in their sepal characters. *T. ovatum* was originally described from Washington, and extends southwards into northern California in Humboldt and Mendocino Counties. Specimens belonging to it also occur apparently in Santa Cruz County. It differs from the variety *stenosepalum* chiefly in that the petals turn pink in drying and the sepals are broader. The two forms overlap in Washington State, but the variety extends further east and south. In certain intermediate areas there appear to be transition forms as regards width of sepals, but specimens of the variety from Montana are entirely distinct from specimens of the species proper from Washington. However, certain specimens having sepals of the species do not turn pink in drying, while the petals of typical forms of the variety do occasionally turn pink in drying. Hence it seems necessary to regard the variety *stenosepalum* as a transitional variety.

Apparently continuous intermediate series occur between all three forms, *T. ovatum*, the variety *stenosepalum*, and *T. venosum*, in intermediate geographic areas. This appears to be a case of continuous geographic variation, yet in their typical form they are so different that all three forms require separate recognition. The sepal differences are the most conspicuous, the sepals varying from 2 cm. wide with 3 prominent nerves in *T. venosum*, to 3 mm. wide without visible nerves in var. *stenosepalum*.

Specimens examined:

Montana: Helena, 1891, *Alderson* (E. Starz, Herb. Whelpley), two specimens (Mo. Bot. Gard. Herb.), TYPE.

Idaho: Paradise Hills, Latab Co., April 18, 1900, *Le Roy Abrams* 548 (Univ. Cal. Herb., 13751); Lake Waha, Nez

Perces Co., June 3-4, 1896, *A. A. & E. G. Heller 3182* (Univ. Cal. Herb., 119597).

Oregon: Yamhill River, Yamhill Co., May, 1879, *Mrs. R. W. Summers* (Univ. Cal. Herb., 72174).

Washington: upper valley of the Nesqually, 1894, *O. D. Allen 58* (Univ. Cal. Herb., 119596).

California: near Marble Mountain, Siskiyou Co., alt. 6000 ft., "10 feet from melting snow," June, 1901, *H. P. Chandler 1550* (Univ. Cal. Herb., 30088). The specimens on this sheet are minimum size, leaves  $3 \times 2$  cm., stem 10 cm., sepals 10 mm. long. Head of McCloud River, northeastern Shasta Co., June, 1903, *Hall & Babcock 4134* (Univ. Cal. Herb., 54195); Moraga Valley, Contra Costa Co., Feb. 22, 1888, *E. L. Drew* (Univ. Cal. Herb., 13818); Mt. Tamalpais, Marin Co., April 26, 1893, *J. B. Davy 121* (Univ. Cal. Herb., 3989). This is maximum size, leaves  $14 \times 11$  cm., stem 52 cm. long, sepals  $32 \times 9$  mm. Same locality, Feb. 22, 1894, *J. B. Davy 798* (Univ. Cal. Herb., 3988); Lagunitas Creek, Marin Co., March, 1896, *Alice Eastwood* (Univ. Cal. Herb., 3994); Sequoia Cañon, Marin Co., Jan. 31, 1892, *Michener & Bioletti 2141a* (Univ. Cal. Herb., 142147); west side of King's Mountain, San Mateo Co., March 18, 1902, *C. F. Baker 329* (Univ. Cal. Herb., 142146); Santa Cruz Mountains, March, 1896, *M. S. Baker* (Univ. Cal. Herb., 72280).

The following range for var. *stenosepalum* can be deduced: western Montana and southern Washington to middle California (Santa Cruz Mountains). The type of *T. ovatum* is somewhat more northerly.

26. **T. nivale** Riddell, Syn. Fl. West. States, 93. 1835; Baker, in Curt. Bot. Mag. *pl. 6449*. 1879; Selby, in Jour. Hort. Soc. 5: 36. *pl. 3*. 1890.

This species is so distinct that it is impossible to confuse it with any other. It is probably a derivative from *T. grandiflorum* or from the species from which the latter was derived. The petals are said to be sometimes green,<sup>1</sup> or striped with

<sup>1</sup> Traill, C. P. Studies of Plant Life in Canada, 36. 1906.



red and green, and the petioles of the leaves vary much in length.

In *T. nivale* Riddell the peduncle may be erect, declined or nodding, as in the three species, *T. erectum*, *T. declinatum*, and *T. cernuum* respectively. These conditions in *T. nivale* probably represent unit varieties which would breed true in cultivation, and it is reasonable to suppose that the differences between the above three species have also originated through unit variations. *T. nivale* and *T. rivale* are the most aberrant of the North American *Trillia*. The dwarf character of both may be supposed to have originated through mutations. The leaves of *T. nivale* most nearly resemble in shape those of *T. viride* Beck, though much smaller. In the latter, however, both the leaves and flowers are sessile, while in *T. nivale* the leaves are short-petioled and the flowers rather short-peduncled, so that a close relationship cannot be assumed.

*T. nivale* differs chiefly from its probable ancestor, *T. grandiflorum*, (1) in being a dwarf, (2) in the shape of the leaves, which are oval, obtuse, with short petioles, instead of rhombic-oval, acuminate, sessile, and (3) in the shape of the petals, which are oblong or oval instead of oblanceolate or obovate-oblanceolate and mucronate. If we compare these differences with those between *Oenothera Lamarckiana* and its dwarf mutant *Æ. nanella*, we see that the differences (1) and (2) above might have originated at one stroke, though as regards (2) the condition is reversed, for in *Æ. nanella* the leaves are mostly sessile, while in *Æ. Lamarckiana* they are petioled. The difference (3) in the petals of *T. nivale* would probably have required another and independent step. At any rate, although the species is so aberrant in the genus, two mutations are sufficient to account for its origin. According to the older views, one must have assumed a long period of isolation and gradual selection to produce such a form. Now we know that there is no necessary relation between the length of a step and the time taken to produce it. A relatively wide mutation will happen just as quickly as a narrow one, and, indeed, if the wider difference has any survival value it

will lead to the supplanting of the original type more quickly than when the step is a narrow one.

Western Pennsylvania to Ohio and southeastern Minnesota, south to Kentucky and Nebraska.

**27. *T. rivale* Wats. Proc. Am. Acad. 20: 378. 1885.**

This species has perhaps been derived from *T. ovatum* through a dwarf mutation and other changes, in the same way that *T. nivale* has probably been derived from *T. grandiflorum*. Like *T. nivale* it is a dwarf, but here the resemblance ceases except that the leaves are petioled. It resembles *T. ovatum* in its recurved stigmas, but differs in every other part. The leaves of *T. rivale* are not only very much smaller but they are ovate (not rhombic-ovate), rounded or subcordate at base (not cuneate), and petioled (not sessile). The flowers are much smaller, the sepals more broadly lanceolate, the petals subrhombic, narrowed to a claw, white but speckled with purple near the center.<sup>1</sup> In *T. ovatum* the petals are white, soon changing to rose color and dark red. The distinctions of *T. rivale* are so numerous that it is not profitable to conjecture further concerning its origin. The extremes of size variation observed are as follows: stems 8–24 cm. long, 1–3 mm. thick, peduncle 6–8 cm. long, leaf-blade 3–7 cm. long, 1.7–4 cm. wide, petiole 6–23 mm. long, sepals 9–15 mm. long, 5–8 mm. wide, petals 15–27 mm. long.

In the coast mountains of northern California and southern Oregon.

**28. *T. Catesbaei* Ell. Sketch 1: 429. 1821.**

*Solanum triphyllum*; flore hexapetalo, carneo Catesb. Nat. Hist. Car. 1: 45. pl. 45. 1771.

*T. cernuum* L. Sp. Pl. 339. 1753, in part.

*T. nervosum* Ell. Sketch 1: 429. 1821; Lodd. Bot. Cab. 19: pl. 1860. 1832.

*T. stylosum* Nutt. Gen. 1: 239. 1818.

This species and *T. affine* are markedly different from the other pedunculate species of *Trillium*. In them the stigmas

<sup>1</sup> According to Howell (Fl. N. W. Am. 1: 661. 1902), this is apparently present in some specimens and absent in others.

are united at the base into a short style, a peculiarity which has appeared apparently independently in *T. pusillum*. The nearest relative of *T. Catesbaei* is probably *T. cernuum*, from which the main distinctions are as follows: In *T. cernuum* the leaves are rhombic, 3-nerved, acuminate, and more or less cuneate at the base; in *T. Catesbaei* they are elliptic or oval, 5-nerved, acute or acuminate, and constricted at the base into a short petiole. The peduncle is nodding in *T. cernuum*, and strongly recurved or sometimes declined in *T. Catesbaei*. The petals in *T. cernuum* are elliptic, oval or ovate, about 2 cm. long, acute or obtuse, revolute, white or pink; in *T. Catesbaei* they are oblong or oblong-lanceolate, reaching more than 4 cm. in length, obtuse or abruptly pointed, crisped, recurved, pink or rose-color. In *T. Catesbaei* the stamens are much longer, reaching 18 mm. (8 mm. in *T. cernuum*), and the filaments are longer than the bright yellow recurved anthers. Yet another difference exists in the absence of a style in *T. cernuum* and its relatives.

In woods, North Carolina and Tennessee to Georgia and Alabama.

**29. *T. affine* Rendle, Jour. Bot. 39: 334. 1901.**

This species is known only from specimens collected by Rugel in Georgia. It evidently belongs with *T. Catesbaei* from which it is differentiated, according to Rendle, by its "broader sepals, smaller not undulate petals, shorter stamens, and leaves broader above the middle." The filaments in particular are only about 4 mm. long. *T. affine* recalls *T. cernuum* in size and habit of leaf and flower, but like *T. Catesbaei*, differs in its longer stamens exceeding the stigmas, and in the union of the latter at the base.

**30. *T. venosum* Gates, n. sp.**

Plate 6, fig. 1.

Herba caule robusto, foliis ovato-rhomboideis, 5-7-nerviis, breviter acuminatis; pedunculo erecto; sepalis oblongo-lanceolatis, 3.5-5.8 cm. longis, 14-20 mm. latis, 3-5-nervatis; petalis albis, ovato-oblongis, marginis crispis; antheris rubicundis, apicibus foras curvatis, stigmata superante; stigmati-

bus divergentibus apicibus recurvatis ovario flavo excedentibus.

Stem stout, 5–10 mm. in diameter, 2–3.5 dm. high, purplish, sheathed at base for a distance of 6 cm.; leaves rhomboid-ovate, 5–7-nerved, 6–11 cm. long, 5–8 cm. wide, acute, short-acuminate; peduncle 3 cm. long, erect, purplish, 2 mm. thick; sepals large, and with 3–5 prominent veins, oblong-lanceolate, broad-pointed, 3.5–5.8 cm. in length, 14–20 mm. in width; petals white, ovate-oblong, obtuse-pointed, with crisped margins, 3.5–5.5 cm. long and 1.4–1.5 cm. wide; anthers 8–15 mm. long, bright pink, curved outwards at the summits, slightly surpassing the stigmas, filaments about 5 mm. long, dilated at base; stigmas slender, 10 mm. in length, somewhat divergent, recurved at the tip; ovary yellow, about 10 mm. long.

This species is nearest *T. Scouleri*, of which I have not seen specimens. In Rydberg's description of that species the sepals are not mentioned, but the large conspicuously veined sepals of *T. venosum* could scarcely have been overlooked had they been present on Rydberg's species. The present species is intermediate between *T. grandiflorum* and *T. ovatum* in size and shape of petals and length of anthers. In specimens of *T. grandiflorum* from the more western part of its range, e.g., Milwaukee, Wis., the sepals are 5-nerved but they are much narrower and the veins are less prominent than in *T. venosum*.

The main distinctions of *T. venosum* from *T. Scouleri* are in the broad sepals with their prominent veins, the pink color of the anthers, and the 5 rather prominent veins of the leaves. The petals appear to resemble closely those of *T. grandiflorum* in several features.

Specimens examined:

Dry Buck, Boise Co., Idaho, 10 May, 1911, *J. Francis Macbride* 847 (Mo. Bot. Gard. Herb. and Univ. Cal. Herb., 163236), TYPE. I reproduce here the cotype specimen because it is larger than the type specimen and shows the characters better.

The following specimens come nearest to *T. venosum* but differ in certain features:

Cuprum-Peacock Mine road, Seven Devils Mountains, Idaho, alt. 7000 ft., July 11, 1899, *W. C. Cusick 2232* (Univ. Cal. Herb., 3986). In this species the petals turn purplish, as in *T. ovatum*, and the leaves have short petioles (6 mm.). Five miles from Crescent City, Del Norte Co., Cal., April 2, 1902, *P. E. Goddard 309* (Univ. Cal. Herb., 30086), petals  $7 \times 3$  cm. (resembling *T. grandiflorum*), sepals 5 cm. long by 12 mm. wide, leaves 10 cm. long by 8.5 cm. wide.

The following, with very large, broad, subacute petals, broad, unnerved sepals, and very broad rhomboid leaves, fits neither *T. venosum* nor *T. ovatum*, and should be considered as distinct: Eureka, Humboldt Co., Cal., April 13, 1913, *J. P. Tracy 4034* (Univ. Cal. Herb., 176190), petals  $60 \times 35$  mm., sepals  $40 \times 19$  mm., obtuse, leaves 15 cm. wide by 14 cm. long, stem stout. This specimen appears to resemble *T. Scouleri*.

**31. *T. obovatum* Pursh, Fl. Am. Sept. 1: 245. 1814.**

*T. grandiflorum* var. *obovatum* Farwell, Eleventh Ann. Rept. Comm. Parks and Boul. Detroit, 53. 1900.

This plant, according to Farwell, differs from *T. grandiflorum* in having much smaller petals which are rose or pink. His plants may really belong to var. *parvum*. Reichenbach's plate and description,<sup>1</sup> under the name *T. obovatum* Pursh, of plants collected in Kamtschatka and communicated by Ledebour, represent a distinct plant, differing from *T. grandiflorum* especially in having shorter peduncle, petals white, pale rose color, or lavender, very short filaments and style, stigma subcapitate, the very short lobes reflexed. It is undoubtedly distinct from *T. obovatum* Pursh and *T. Kamtschatikum* Pall.,<sup>2</sup> differing from the latter in certain minor features. Pursh's original plants were from Montreal, and a study of the species should be made in that vicinity. Its exact characters cannot be understood until this is done. Rydberg, in his 'Flora of Montana,'<sup>3</sup> records *T. obovatum*

<sup>1</sup> Ic. Bot. Exot. 1: 21. pl. 29. 1827.

<sup>2</sup> Ledebour, C. F. Fl. Ross. 4: 121. 1853. See also Rendle, Jour. Bot. 39: 329. 1910.

<sup>3</sup> Mem. N. Y. Bot. Gard. 1: 102, 472. 1900.

Pursh with the statement that it is distinguished from *T. ovatum* Pursh by its obovate, white, or rose-colored petals.

The relationships of the species of *Trillium* seem complex and confusing because of the numerous cross-relationships which appear. But the difficulties of interpretation are, I believe, considerably clarified when we realize (1) that particular elements of the germ-plasm vary independently of each other and that (2) the variation of a single germinal element may affect the external morphology in various parts of the organism. The application of these two principles helps to clear up what may otherwise become a hazy maze of relationships. This is particularly true of large genera, in which the number and diversity of species greatly exceed that of *Trillium*.

The genus is naturally divided into two groups having respectively pedunculate or sessile flowers. Whether the sessile-flowered gave rise to the pedunculate group or *vice versa* is difficult to say, but it appears probable that the transition from one condition to the other occurred but once (presumably through a mutation) since there appear to be no cross-relationships from one group to the other. I mean by this that the members of each group may be considered to be descended from one ancestor, and e.g., none of the characters of the pedunculate group are such as might have been derived from particular members of the other group. On the contrary, within each group parallel mutations have probably taken place, as in the dwarf origin of *T. rivale* and *T. nivale*.

#### VARIATION OF TRILLIUM

The genus *Trillium* has long been known to botanists and horticulturists for its variability. Nearly all parts of the plant vary, particularly the shape of leaves and petals, and the color of the petals. On the other hand, the size of the plant and the relative length of filaments and anthers is usually constant within certain limits, and the latter is frequently used as a specific differential, though it too is subject to some variation. The number of members in the whorls

of leaves or flower parts also varies, as well as (rarely) the number of whorls. Teratological variations are relatively abundant and have been described in many of the species, particularly *T. grandiflorum* Salisb., *T. erectum* L., and *T. sessile* L. A number of these records have been brought together below, and a more exhaustive search in semi-popular journals would doubtless add to the list.<sup>1</sup>

Cowles, S. N. *Am. Nat.* 3: 102. 1869.

At Otisco, N. Y., two specimens of *T. erythrocarpum* Michx. with pistillate flowers and 9 petals were collected. The extra petals replaced the stamens and were somewhat smaller than normal.

Matthews, G. F. *Am. Nat.* 3: 382. 1869.

At St. John, N. B., one specimen of *T. erythrocarpum* Michx. was gathered with 4 leaves, 4 sepals, 4 petals, and 8 stamens.

Fisher, R. A. *Am. Nat.* 4: 46. 1870.

At Arba, Ind., one specimen of *T. sessile* L. was found with parts in fours, and one specimen of *T. recurvatum* Beck with 2 leaves, 2 sepals, 2 petals, 4 stamens, 2 stigmas.

Hankenson, E. L. *Bull. Torr. Bot. Club* 1: 21. 1870.

*T. grandiflorum* at Newark, Wayne Co., N. Y. "Forms found here have petals more or less turned to green, with long petioled smaller leaves, borne lower down on the stem; or with stem leaves *entirely wanting*, and a single radical leaf instead. The calyx of the leafless stemmed form appears larger and more leafy."

Hall, I. H. *Bull. Torr. Bot. Club* 1: 21. 1870.

*T. erectum* L. var. *album* Pursh, in central and western New York. The author thinks the variety *album* and normal red may appear from the same rootstock in successive years. The variety *album* is normally a starveling, smaller. The color of the petals varies from creamy yellow or greenish white to the normal purple, sometimes with a blush of purple

<sup>1</sup> Certain of these facts were referred to elsewhere. See Gates, R. R. Teratology and phylogeny in the genus *Trillium*. *Science* N. S. 42: 879. 1915.

in central part of the petal, sometimes with faint, streaky tinges of purple lengthwise of the petal, though not at all like *T. erythrocarpum* Michx. It has also less scent. Hall thought it was simply an unhealthy state of *T. erectum*.

*T. erectum* frequently occurs with the peduncle bent down under the leaves as in *T. cernuum* L. The peduncle is sharply bent at an angle just above the leaves, and not merely curved or drooping.

Hall, I. H. Bull. Torr. Bot. Club 1: 36. 1870.

A plant of *T. erectum* var. *album* Pursh dug up has kept its "creamy green" color every year for 5 or 6 years.

Osborne, C. S. Am. Nat. 4: 125. 1870.

At LeRoy, N. Y., *Trillium* sp. was seen with 2 stems from the same rootstock; one had petals and sepals alike except for the white margin to apex of petals, and the other had petals oblong, pure white with narrow green stripe down the center.

Coleman, N. Bot. Gaz. 2: 90. 1877.

The author found one specimen of *T. grandiflorum* having 4 leaves, 4 petals, 4 sepals, 4 stamens, 2 stigmas, and a 4-angled ovary, and a specimen of *T. erythrocarpum* var. *Clevelandicum* Wood having 6 sepals and 15 petals, all green.

Gray, A. Am. Jour. Sci. 15: 153. 1878.

*T. erythrocarpum* Michx. with polymeric flowers, found by Pastor J. H. Wibbe near Oswego, N. Y., has been a constant feature since discovered "five years ago." The specimen in Gray Herb. is described by Deane (*vide infra*). It has 8 sepals (one with a white petaloid growth attached), 8 petals, at least 20 stamens, and a whorl of 7 leaves, one of which is forked at the tip.

Gray, A. Two remarkable forms of *Trillium*. Bull. Torr. Bot. Club 6: 272. 1878.

Two specimens from St. Louis, Mich. are described: one of *T. grandiflorum* with petioles to the leaves and a green



stripe down the center of the petals; the other having similar petals and enlarged foliaceous sepals but no whorl of leaves. Further records of this var. *variegatum* in Bull. Torr. Bot. Club 6: 277-278. 1878.

Smith, Erwin T. A Michigan Trillium. Bot. Gaz. 4: 180-181. 1879.

*T. grandiflorum* var. *variegatum* is described. It differs chiefly from the species in having a greenish stripe down the center of the petals, which are typically obovate-mucronate, leaves long-petioled, broadly ovate, acuminate, and ovary green. It was found to occur commonly every year and to be well distributed. It is very variable in shape of petals, length of petioles, etc., and the stem also may be leafless or the calyx enlarged to form leaves.

This remarkable condition of *T. grandiflorum* has since been found and studied in a number of localities, though it has not usually been known under the name var. *variegatum*.

Wright, S. H. Bot. Gaz. 4: 232. 1879.

The author found the above form at Penn Yan, N. Y., and received specimens of it from Lockport, N. Y.

James, J. F. Bull. Torr. Bot. Club 10: 57. 1883.

At Cincinnati, Ohio, was found a specimen of *T. sessile* which was pentamerous—5 leaves in a whorl, 5 sepals, 5 petals, 8 stamens, 4 stigmas, 4-celled ovary, one of the petals having an anther on one side.

Tracy, Mrs. C. T. Bull. Torr. Bot. Club 10: 71. 1883.

At Ripon, Wis., a plant of *T. cernuum* L. was discovered with one of the sepals replaced by a leaf, and two of the petals with a green stripe through the center.

James, J. F. Bot. Gaz. 9: 113. 1884.

A plant of *T. erectum* L. was found, which was tetramerous, having an extra leaf on the stem above the whorl of three, 4 sepals, 4 petals, 8 stamens, 4 stigmas, and a 4-celled ovary.

Two of the sepals were half green, the other half colored like the petals.

Dudley, W. R. Bull. Cornell Univ. 2: 99. 1886.

Dudley records a plant of *T. erectum* L. with green flowers, and one of *T. grandiflorum* Salisb. showing synanthly and virulence, the double form being cultivated.

Fermond, Ch. Essai de phytomorphie 2: 298. Paris. 1886.

The author speaks of isolation and displacement of single leaves.

Foerste, A. F. Bot. Gaz. 16: 163. 1891.

A specimen of *T. sessile* L. is described having a whorl of 4 leaves, and flower parts in threes but partly arranged as though in fours, i.e., a sepal takes the place of a petal, and one segment is half sepal, half petal.

Foerste, A. F. Bot. Gaz. 19: 460-465. 1894.

The following conditions in *T. sessile* L. from Dayton, Ohio, are carefully described, showing the phyllotactic arrangement of parts: (1) leaves and flower parts all in fours, tetramerous; (2) partly with leaves decussate in pairs, stamens and stigmas in threes, other abnormalities; (3) a similar condition with an apparent "attempt to maintain a quaternary phyllotaxy, after numerically they have gone over to the normal ternate form"; (4) whorls of parts 3, 4, 3, 4, 3, 4, but quaternate position maintained even when the number of parts is 3.

The detailed description of one of the specimens is as follows: "A pair of opposite broader leaves, followed in decussating order by a pair of narrower leaves," an outer and an inner pair of sepals, then 4 petals decussating with the two sets of sepals taken as a whole, 4 outer stamens, 4 inner stamens, and an ovary with 4 styles.

Osband, Lucy A. Am. Nat. 28: 706. 1894.

At Ypsilanti, Mich., was found a plant of *T. grandiflorum* Salisb., double, having 2 sets of sepals and 2 of petals, the

outer petals striped, except one which was half white, the inner petals white except a thread of green through the center of one; stamens and ovary also abnormal.

Owen, Maria L. Bot. Gaz. **19**: 337-338. 1894.

Specimens of *T. cernuum* L. from Canobie Lake, N. H., with the following peculiarities, were found:

1. About an inch above the normal leaf whorl were 3 whorls of 3 leaves, each close together, forming a rosette; flower erect, rather large, petals  $11 \times 4$  lines, with a white stripe down the center and a green one on each edge; stigmas 4; one petal 2-parted.

2. Above the normal whorl 2 whorls close together, and a third extra whorl  $\frac{1}{2}$  inch above this, at the base of the flower; petals green and white; one stamen abortive; stigmas 2. Several similar specimens collected from the same locality.

Eastwood, Alice. Erythea **4**: 71. 1896.

The following three abnormal specimens of the white-flowered form of *T. giganteum* were found in the San Bruno Hills of San Mateo Co., Cal.: (1) with four leaves, "all parts of the flower in fours even to the ovary," stamens 8; (2) with six leaves (not stated whether these were in 1 whorl or 2), 6 outer divisions of the perianth and 5 inner, 10 stamens, and 6 cells to the ovary; (3) one of the outer perianth segments a "true leaf," symmetry otherwise normal.

Smith, Arma A. Abortive flower buds of Trillium. Bot. Gaz. **22**: 402-403. 1896.

Davis, C. A. Trillium grandiflorum (Michx.) Salisb.; its variations normal and teratological. Proc. Am. Assoc. Adv. Sci. **46**: 271-272. 1898.

Nearly all the variations found in this species are described.

Kellerman, Mrs. W. A. Asa Gray Bull. **6**: 18-20. fig. 4-5. 1898.

Mrs. Walker found a double specimen of *T. grandiflorum* Salisb. growing in woods in Jefferson County, Ohio. She re-

moved it to her garden where it bloomed for 10 years, always producing the double flower. The root afterwards was divided, and one portion produced 3 stems, all with double flowers. Two of these were dissected, one having 9 whorls, the other 13 whorls of petals in cycles symmetrically alternating. The stamens and pistils were almost completely aborted and there were no seeds. Except for this doubling, the plants were normal.

Macoun, James M. Canadian Rec. Sci. 7: 476. 1898.

Monstrosities of *T. grandiflorum* Salisb. are not uncommon in southwestern Ontario. These evidently refer for the most part to var. *variegatum* Smith. A fine series was examined from Mr. J. Dearness, London, Ont., Mr. R. Cameron, Niagara, Ont., Mr. J. M. Dickson, Hamilton, Ont., and Mr. Wm. Scott, Toronto, Ont. Mr. Dickson found that they occurred in different years in the same locality and noted the following types:

1. Several with white edgings and markings on the sepals. The most remarkable had 1 sepal green, 1 half green, half white, and 1 pure white; sepals and petals spirally inserted; leaves normal.

2. Leaves and sepals normal; petals marked with green lines or bands towards the base.

3. Leaves and sepals normal; petals green with a narrow white margin.

4. Leaves distinctly petiolate; petioles 1-3 inches long; sepals white with a green stripe down the middle; petals narrowed, lanceolate, white with a broad green band in the center from base to apex.

5. Leaves as in the former type; sepals normal; petals obovate, apiculate, long-clawed, with broad green centers and white margins.

6. Leaves ovate, long, acuminate, petioled; petioles ascending, widely spreading, 7 inches long, inserted about 2 inches above the rootstock and 6 or 7 inches below the flower; sepals normal; petals green with white margins. All the flowers appeared to be perfect, though there was an occasional

sterile filament. One plant, evidently representing the type of var. *variegatum*, was photographed, and a drawing from the photograph was published in the 'Plant World,' vol. 6, page 88.

Among the plants sent to Mr. Macoun by Mr. Cameron from Niagara was one with its petals changed into petioled leaves (petioles over 1 inch long). Mr. Cameron also collected and photographed a plant found on Navy Island, Niagara River, in 1896, very large-flowered, having 21 pure white petals. The root was transplanted, and in 1897 produced 2 flowers, each having 21 petals. This is very good evidence showing how closely these things come true in vegetative reproduction. The same collector also reported a double yellow-flowered dwarf specimen from Niagara Falls, which probably belonged to another species.

Several sheets of specimens in Mo. Bot. Gard. Herb., collected by Mr. William Scott in the Don Valley near Toronto, in 1896, belong to *T. grandiflorum* var. *variegatum* and show a great range of variation.

Holzinger, John M. A green Trillium. *Plant World* 4: 132. *pl.* 9. 1901.

*T. grandiflorum*, collected at Winona, Minn., had its flower parts all green, 6 whorls of 3 leaves each, no stamens or carpels.

Pollard, Chas. L. Double Trilliums. *Plant World* 4: 213. *fig.* 1. 1901. (Reprinted from *Asa Gray Bull.* 6: 18-20. 1898.)

No new record, merely a comment on Mrs. Kellerman's record. This differed from the above in having the parts colored, hence "double" in the ordinary sense.

Rendle, A. B. *Jour. Bot.* 39: 331. 1901.

The author mentions a specimen of *T. grandiflorum* from Goat Island, Niagara (not Nicaragua), whose leaves have petioles 1 cm. long, and another specimen a "monstrous form" from Syracuse, N. Y. (from Gray Herb.), with leaf stalks as much as 3 cm. long.

Bishop, Irving T. *Plant World* 5: 11. 1902.

A variety of *T. grandiflorum* was noticed to be common near Buffalo, N. Y., students obtaining many specimens every spring. (This is evidently the var. *variegatum*). The petals become more or less green and bract-like, the leaf-blade smaller, and the petiole and peduncle become longer. In some cases the peduncle is longer than the rest of stem; in others, the petiole is 4-6 inches long, with a narrow lanceolate blade 3 inches long. Multiplication of organs is common, extending to petaloid and bract-like forms and also to the leaves. In *T. erectum* L., in few cases, the whorls are repeated, but in no case is there lengthening of leaf- and flower-stem.

Britcher, H. W. Variation in *Trillium grandiflorum* Salisb. *Me. Agr. Exp. Sta. Bull.* 86: 169-196. *pl.* 9-13. 1902.

This is a careful study of the variation in the plants found in quantity near Syracuse, N. Y. Hundreds of thousands of plants grow there, thousands of them abnormal, perhaps 10 per cent. In some spots barely a half-dozen are abnormal among thousands of plants; near-by 10-15 per cent may be abnormal. In typical plants the petals vary from narrow and pointed to broad and obtuse, but always mucronate.

An elaborate series of measurements is given for 185 plants, with notes on their peculiarities. In addition to the other conditions described, Britcher found that the petals, sepals, or ovary might be stalked.

Only the range of these remarkable variations can be recorded here. The petals varied in color "from typical white or pink, through white with green center stripe to solid green." Green petals or portions of petals are usually persistent, gradually becoming purplish brown in color. The abnormal plants have usually entirely disappeared by the time the carpels of the normal plants have attained their full size. This is interesting as showing that the abnormal forms do not reproduce themselves by seed and must therefore arise by repeated mutations from the normal forms.

The stem may be wholly absent or as much as 34 cm. in length. The leaves vary from sessile to petiolate with petioles

16 cm. long. The peduncle varies from 2 to 220 mm. in length. The sepals may be sessile or on stems 44 mm. long, and similarly the stalks of the petals may reach 64 mm., the ovary stalks 23 mm. The stem-leaves are sometimes absent.

From the fact that the same rootstock produces the same peculiar condition year after year, as has been shown by transplanting the specimens, it is evident that the various abnormal conditions are inherited and not environmentally produced, as has been so frequently conjectured; though the type of abnormality produced by a given rootstock will perhaps vary within limits from year to year. It would be interesting to know what these limits of variation are for individual rootstocks showing different stages of the abnormality.

Hopkins, Lewis S. A rare freak of the Trillium. *Plant World* 5: 182-183. *fig. 1.* 1902.

In Troy, Ohio, was found *T. sessile* L. with three stems arising together from rootstock. The first stem had 3 whorls of 3 leaves each, the lower 2 crowded together, 4 petals, no sepals, 5 stamens, 3 styles and stigmas, and ovary 6-angled. The second stem had 2 whorls of 3 leaves each, no sepals, 6 petals, 7 stamens, 4 styles and stigmas, and 8-angled ovary. The third stem had leaves as in the second, but 3 sepals, 6 petals, 9 stamens, 2 styles and stigmas.

Morris, E. L. "Occasional" leaves of Trillium. *Plant World* 5: 92-93. *pl. 13.* 1902.

Near Washington, D. C., was found a plant of *T. sessile* L. bearing two single leaves with very long petioles, direct from the rootstock.

Morris, E. L. Abnormal Trilliums. *Plant World* 6: 87-89. *fig. 1.* 1903.

This figure is a plant of *T. grandiflorum* var. *variegatum* from Hamilton, Ont. Two specimens from Moose Head Lake, Maine, 1898 (Aug.), collected by G. B. Grant, "have the simple leaves long-petioled from the rootstock." Probably these free, single, long-petioled leaves are an extreme case

of the *variegatum* condition with long-petioled leaves from near the base of the scape.

Beattie, F. S. *Rhodora* 7: 40. 1905.

A specimen of *T. undulatum* Willd. from Gloucester, Mass., had two stems from one rootstock. One of the flowers had one of its sepals enlarged to  $\frac{5}{8}$  the length of ordinary leaves and the shape nearly that of a leaf. At Rowe Pond, Somerset Co., Me., twin stems in this species were found to be the rule.

Gary, Lester B. Variation in *Trillium*. *Plant World* 8: 257–259. 1905.

A plant of *T. erectum* with cream-colored petals and diminished odor, but ovary red, was found in the gorge near Niagara whirlpool where *Trillium* is abundant.

The various common variations of *T. grandiflorum*, green petals, long petioles, etc., are described.

Andrews, F. M. Some monstrosities in *Trillium*. *Plant World* 9: 101–102. *fig. 17*. 1906.

The following are described:

One specimen of *T. sessile*, with all stamens and carpels transformed into floral leaves, 14 in number.

All stamens and carpels of a plant of *T. recurvatum* transformed into floral leaves, larger than normal, 23 in number.

One specimen of *T. sessile*, with 4 leaves, 3 small sepals, 4 large, partly greenish petals, 6 small stamens and styles.

Other specimens of these two species had a sepal and petal “grown together,” partly or wholly, one half green, the other half colored (cf. Foerste). Similar observations were made with other species.

One specimen of *T. erectum* with 3 leaves, 3 sepals, 5 petals, 4 stamens, 2 styles.

Slight deviations, in tendency to union of floral parts in *T. nivale*.

Clute, W. N. A remarkable change of color in *Trillium*. *Am. Bot.* 14: 33–35. 1908.



In 1907 a number of plants of the red *T. erectum* were sent to Joliet, Ill., from New Britain, Conn., some of them being still in flower. They were set out and flowered in 1908, but all the flowers but one were white, this one having only a trace of red on the stamens.

Deane, Walter. *Rhodora* 10: 21-24. 1908.

At Squam Lake, Holderness, N. H., Mr. DeMeritte in 1907 found two stems of *T. undulatum* Willd. growing together and having the same peculiarities. They possessed 3 whorls of 3 leaves each, separated by internodes. The leaves on one of the specimens, which was collected, are carefully described and measured.

Two specimens of the same species from Brunswick, Me., in Gray Herb., collected by Mr. Swallow, but without date, show in other cases sepals leaf-like, ovate, and taper-pointed, 8.2-9.2 cm. long. Another specimen in Gray Herb., collected by Miss K. L. Kimball at Fitzwilliam, N. H., in 1891, has its leaves, sepals, petals, and styles in fours, the stamens probably 8.

Deane, W. *Rhodora* 10: 214-216. 1908.

In 1908, Mr. DeMeritte found in the same spot as the previous year a cluster of five plants; (a) three of which had 3 whorls of 3 leaves each; (b) one had 2 whorls of 3 leaves each; and (c) one had 4 whorls of 3 leaves each; in addition, another plant (d) at a little distance had a whorl of 4 leaves.

(b) This plant had sepals 9 cm. long resembling leaves, 4 petals (two formed by chorisis), 3 stamens (opposite the petals), 3 styles, ovary 2-celled.

(c) In this plant the petioles of the lowest whorl of leaves were 7 cm. long, and there were 3 large sepals 5 cm. long, 3 stamens (opposite the sepals), 3 styles, ovary 1-celled.

(d) One of the 4 leaves had a broadly winged petiole; there were 4 sepals, 3 petals, 6 stamens, 4 styles, ovary 4-celled.

In 1897, at Farmington, Me., Mr. C. H. Knowlton collected a specimen of *T. undulatum* having a whorl of 4 leaves with

all the other parts in threes, one stamen more or less petaloid, and the ovary 1-celled with three parietal placentae.

A specimen of *T. undulatum* in Mo. Bot. Gard. Herb., collected by Dr. J. M. Greenman at Mt. Mansfield, Vt. (Plants of Vermont, No. 1253), 2–4 July, 1897, has a whorl of 4 leaves. There are apparently 4 sepals and 4 petals in the flower, but the number of stigma lobes is 3.

Deane, W. *Rhodora* 12: 163–166. 1910.

In this record Mr. De Meritte examined in 1909 the same spot visited in the two previous years. He found (a) 3 plants having 3 whorls of 3 leaves each, separated by internodes, and a perfect flower; (b) 1 plant having 2 whorls of 3 leaves each and a double flower. One of the plants in (a) was collected and carefully described by Mr. Deane. Two of the leaves in the uppermost whorl had a lobe on one side, while the third was notched; the ovary was 1-celled with 3 parietal placentae. The plant (b) possessed 3 sepals, 6 petals; of the latter, two in the outer row had a broad green band running down the center, the third a narrow light green line down the center, and the rest were normal in color; ovary 2-celled.

A specimen of *T. erectum*, collected at Glen Road, N. H., is described. The parts were as follows: a whorl of 4 leaves; 5 sepals green with an edging of maroon, 2 also streaked with maroon; 4 petals and a vacant space for the fifth; 8 stamens, 1 with the anther partly doubled; ovary 8-winged, 1-celled.

Deane, W. *Rhodora* 13: 189–191. 1911.

A specimen of *T. ovatum* Pursh, collected by Mr. W. T. Putnam at Lake Cushman, Wash., had 24 petals in regular alternating cycles of 3 each, pink and white instead of purple, no stamens or pistil. Deane also cites Prof. Wm. R. Dudley,<sup>1</sup> who obtained from Woodwardia Swamp Woods a double *T. grandiflorum* having about 14 parts to the perianth.

In a collection of rootstocks of *T. grandiflorum* var. *parvum*, from Exeter, N. H., which were dug up in 1914 and which were potted and bloomed at the Missouri Botanical

<sup>1</sup> Cayuga Flora, 99. 1886.

Garden in March, 1915, one rootstock is of teratological interest. It produced three stems exactly alike. In every case the flower and peduncle were entirely absent, and there was a whorl of 6 rather small (about 5 cm. long), nearly equal leaves. This rootstock has been marked and will be observed to determine whether the same abnormality occurs every year.

It is evident that most of these scattered records were unknown to those who recorded their own observations. It is therefore useful to bring a number of them together, and no doubt this list can be considerably added to. *T. grandiflorum* appears to be the most variable of all in certain localities, and it is obvious that in the different districts where studies have been made, much the same series of variations and teratological malformations have been encountered, though the forms with the stalked petals or ovary appear to be more restricted. It is proven that these are not environmentally produced, at least in the sense that their recurrence from the same root year after year is independent of environment. We can only suppose that such rootstocks have been produced from particular seeds in which a mutation had occurred, giving rise to one of the many aberrant conditions found. The species is in an unstable condition in the same sense in which I have used that term for *Oenothera Lamarckiana*. It is possible that cytological study of *T. grandiflorum* might reveal the basis of this unstable condition, as it has done to some extent in *Oenothera*, and a careful study should be undertaken with this possibility in view. It seems evident that *T. grandiflorum* is mutating in much the same sense that the term can be used for *Æ. Lamarckiana*. In *T. grandiflorum*, however, the mutations are for the most part teratological. It is important to discover, if possible, the fundamental difference between the condition of the germ-plasm of *T. grandiflorum* in which the variations are chiefly in number and arrangement of parts, and the condition in *Oenothera* in which the variations are better coördinated — changes occurring simultaneously in all parts usually without dislocation of their relation to each other. It must be supposed that a redistribution

of some of the germinal materials has taken place, but the nature of that redistribution is at present unknown.

Such wide variations in *Trillium* as the formation of long petioles from sessile-leaved species, and the multiplication of the number of the leaf whorls, with internodes between them, are, however, not obviously teratological; and in the former case they are similar to ordinary specific differences in the genus, while in the latter they, if constant, might well serve as the basis of a distinct genus. Thus the long petioles and short stems of *T. petiolatum* furnish its most striking distinction from such species as *T. sessile*, and it is very tempting to assume that *T. petiolatum* was derived from a sessile-leaved, long-stemmed species in the same way that the typical condition of the variety *variegatum* now apparently arises from *T. grandiflorum*. These suggestions may seem to systematists bold, but we have reached a point where our experimental knowledge of variation must be applied directly in any discussion of the phylogeny and relationships of particular species. The known variations of species of *Trillium* furnish a more reasonable basis for an evolutionary reconstruction than hypothetical continuous variations which experiment seems to show are not usually inherited.

#### PARIS L.

The Eurasian genus *Paris* is mentioned here on account of its close affinities to *Trillium*. Just as *Trillium* is chiefly North American, with a few species closely related to *T. erectum* in northeastern Asia and one species (*T. Govaniana* Wall.) in the Himalayas; so *Paris* is almost entirely Asiatic, with one species (*P. quadrifolia* L.) extending into Europe. The genus *Paris* was probably derived from the ancestors of the group of four species, relatives of *Trillium erectum*, occurring in Japan, Manchuria, and eastern Siberia. Some 30 species have been described, mostly from China, but including 3 from Siberia, 3 from Japan, and 2 from Thibet.

Bearing in mind the probable origin of the genus, its differences from *Trillium* are of much interest. The two may be compared as follows:

## TRILLIUM L.

## PARIS L.

Sepals and petals 3 each; petals larger and more or less colored. <sup>1</sup>	Sepals and petals 4-6 each; petals smaller than sepals, sometimes very long and slender.
Stamens 6, filaments filiform, connective not prolonged or only slightly prolonged be- yond the anthers. <sup>2</sup>	Stamens 8-12, filaments short, anthers with an elongated connective.
Ovary 3-celled, or 1-celled with parietal placentation in <i>T. grandiflorum</i> and sometimes in teratological specimens.	Ovary 4-5-celled, or 1-celled with parietal placentation.
Styles 3.	Styles 4-5.
Leaves normally a whorl of 3.	Leaves a whorl of 4 or more.

Several significant facts point to the direct origin of *Paris* from the *T. erectum* group of *Trillium*, probably through *Trillium tetraphylla* Gray and *Paris quadrifolia* L. Comparing *T. erectum* with *P. quadrifolia* the main differences are: (1) the parts in fours instead of threes; (2) the greenish reduced petals of the latter; and (3) the greatly elongated connectives of the anthers. Every one of these conditions is more or less completely duplicated in teratological variations of *Trillium*. Plants with all the parts in fours occur occasionally in a number of species; a virescent condition of the petals is not uncommon; in *T. decumbens* the anther connectives are prolonged beyond the pollen-sacs. The one-celled condition of the ovary in some species of *Paris* is found as a relatively common teratological variation in *Trillium*.

*Paris tetraphylla* Gray<sup>3</sup> forms a transition between the group of *Trillia* closely related to *T. erectum* in northeastern Asia and *Paris quadrifolia*, for its anther connectives agree with those of most species of *Trillium* in not being at all pro-

<sup>1</sup> Except in teratological specimens.

<sup>2</sup> Except in teratological specimens and in *T. decumbens* Harb.

<sup>3</sup> This species is found in China, Japan, and the Himalayan region. See Gray, Asa. Mem. Am. Acad. N. S. 6: 412. 1858-59.

longed. We may therefore assume, as the other facts suggest, that this variation occurred independently of the others, and perhaps subsequently. On the other hand, the reduction in petals in *Trillium* (leading towards *Paris*) displays itself particularly in *T. Smallii* Maxim., in which the petals may be more or less reduced or absent.

The fact that certain teratological conditions in one genus frequently resemble the normal condition in a related genus, as we noted in a previous paragraph, shows that variations tend to follow certain paths. These variations must result from the structure of the germ-plasm, and may be compared with lines of cleavage or fracture. They apparently result from certain weaknesses in the structure of the germ-plasm, and they are apparently not environmentally produced (unless in the sense of large responses to small stimuli), but reappear generation after generation through long periods of time. They represent the unstable nature of certain elements of the germ-plasm, and are apparently, when reproduced from seed, themselves unstable. This is a matter on which more extensive data are urgently needed; e.g., will a 4-parted *Trillium* come true from seed, or how will its peculiarity be inherited, if at all? And will a partly double *T. grandiflorum* which reappears each year from the same rootstalk reproduce itself from seed? It is greatly to be hoped that breeding experiments with teratological plants will be undertaken to determine this point. One is strongly inclined to believe that such peculiarities as polymery and doubling will be reproduced in some, at least, of the offspring. Experiments with double garden flowers of course point to this conclusion.

On the other hand, it appears that somatic variations, such as fasciation, which are not at all inherited in some genera, have become a constant feature of the genus in other genera, e.g., *Celosia*. We have at present no means of knowing how the unstable and non-inherited or partially inherited teratological variations of one genus may give rise to the stable and completely inherited condition of a derived genus; but it is a legitimate interpretation of the facts to suppose that

something like this has happened in the origin of many genera.

The differences between *Trillium* and *Paris* may, as we have seen, be reduced to three; but these, so far as we know from present variations, are apparently independent of each other as a rule. Three mutations are required to account for the origin of a typical *Paris* from a *Trillium* (two if we consider *P. tetraphylla*). Other intermediate species containing one or two of these features only have recently been described by Léveillé from China. Thus *P. Dunniana* Lévl. and *P. aprica* Lévl. also have the anther connectives scarcely, if at all, prolonged, while in *P. atrata* Lévl. the petals are longer than the sepals. We may, therefore, assume a considerable amount of elimination of such forms, perhaps through their own instability in inheritance, until finally a stable combination was reached which has since given rise to the various species of *Paris* through another group of variations. It is greatly to be hoped that some one will undertake crossing experiments with *Paris* and *Trillium*, for they would throw much light on these questions.

#### MEDEOLA Gronov.

A monotypic genus of eastern North America.

**1. *Medeola virginiana* L. Sp. Pl. 339. 1753.**

*Gyromia virginica* Nutt. Gen. 1: 238. 1818; Lamarck, Encyc. Meth. 4: 4. 1796; Illustr. Gen. Tab. 2: pl. 266, fig. 2. 1823; Barton, Elem. of Bot. pl. 14. 1803; Curt. Bot. Mag. pl. 1316. 1816; Meehan, Native Flowers 2: 157. pl. 40. 1879.

Nova Scotia and New Brunswick to Ontario, Minnesota, Florida, and Tennessee.

The genus *Medeola* is remarkably distinct from its nearest relative, *Trillium*, yet there is no question of its affiliation, on the one hand with *Trillium* and on the other hand with *Paris*. The differences enumerated below would seem to indicate that *Medeola* is the sole survivor of a group of North American forms which has disappeared.

In his classical paper<sup>1</sup> in which he compared the flora of eastern North America with that of Japan, pointing out the many striking similarities, Asa Gray regards *Paris hexaphylla* as the Japanese counterpart of *Medeola virginiana* L.

## MEDEOLA Gronov.

## TRILLIUM L.

Deciduous wool on stem.	No wool on stem.
Leaves in 2 (rarely 3) whorls; lower whorl 4–10 leaves.	Leaves in 1 whorl <sup>2</sup> of normally 3 leaves.
Flowers in a sessile umbel, small, greenish yellow.	A single flower, usually dark red or white.
Six perianth segments alike.	Three sepals; 3 petals.

The differences from *Trillium* are much greater than in the case of *Paris*. The presence of 2, or sometimes 3, whorls of leaves recalls a not infrequent teratological condition in *Trillium*, while the variable number of leaves in the lower whorl agrees with the condition in the genus *Paris*. The umbel of flowers is a marked progressive step, while the lack of differentiation of calyx and corolla is a primitive or reversionary condition, again resembling certain teratological specimens in *Trillium*. The fluffy wool on the stems is a positive character of whose origin we know nothing, but there is no reason to believe that it has any selective value.

It is scarcely to be supposed that *Medeola* would cross with *Trillium*, but the attempt would be worth making.

<sup>1</sup> Gray, Asa. Diagnostic characters of new species of phanerogamous plants, collected in Japan by Charles Wright, Botanist to the North Pacific Exploring Expedition. With observations upon the relations of the Japanese flora to that of North America, and of other parts of the northern temperate zone. Mem. Am. Acad. II. 6: 377–452. 1859.

<sup>2</sup> Teratological specimens occur having 2 or 3 whorls.



## EXPLANATION OF PLATE

## PLATE 6

Fig. 1. *Trillium venosum* Gates. From cotype specimen in Mo. Bot. Gard. Herb., collected at Dry Buck, Boise Co., Idaho, by J. F. Macbride 847.

Fig. 2. *Trillium ovatum* Pursh var. *stenosepalum* Gates. From type specimen in Mo. Bot. Gard. Herb., collected at Helena, Montana, by Alderson.



GATES — THE GENUS TRILLIUM

## EXPLANATION OF PLATE

## PLATE 7

Fig. 1. *Trillium giganteum* (H. & A.) Heller var. *chloropetalum* (Torr.) Gates. From specimen in Mo. Bot. Gard. Herb., collected at Humbug Creek, Siskiyou Co., California, by George D. Butler 1168.

Fig. 2. *Trillium luteum* (Muhl.) Harbison. From specimen in Mo. Bot. Gard. Herb., collected at Clemson College, Oconee Co., South Carolina, by H. D. House 1789.

Fig. 3. *Trillium luteum* var. *latipetalum* Gates. From specimen in Mo. Bot. Gard. Herb., collected at Clemson College, Oconee Co., South Carolina, by H. D. House 1789.



GATES—THE GENUS TRILLIUM

## EXPLANATION OF PLATE

## PLATE 8

*Trillium giganteum* (H. & A.) Heller var. *angustipetalum* (Torr.) Gates. From specimen in Univ. Cal. Herb., collected in the foothills near Stanford University, Santa Clara Co., California, by C. F. Baker 306.



GATES — THE GENUS TRILLIUM